

# Estimating competition coefficients in tree communities: a hierarchical Bayesian approach to neighborhood analysis

SHINICHI TATSUMI,<sup>1,†</sup> TOSHIAKI OWARI,<sup>2</sup> AND AKIRA S. MORI<sup>1</sup>

<sup>1</sup>Graduate School of Environment and Information Sciences, Yokohama National University, Kanagawa 240-8501 Japan

<sup>2</sup>The University of Tokyo Hokkaido Forest, The University of Tokyo, Hokkaido 079-1563 Japan

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**Abstract.** Quantifying the strength of competition and understanding how it translates into consequences at the community level are among the key aims of plant ecology. Neighborhood analysis based on the neighborhood competition index has been widely used to estimate species-specific competition coefficients in tree communities. These estimates, however, could not be estimated for rare species with small sample sizes using the conventional species-by-species approach. Here, we develop a new modeling framework for neighborhood analysis in which the competition coefficient is assumed to have a hierarchical parameter structure. Using actual tree census data consisting of 38 species, we demonstrate that the hierarchical model enables us to estimate competition coefficients for all species, including rare ones, within a community. The hierarchical models were selected over the models based on the species-by-species approach as a result of model selection, in either cases where we assumed the competitive strength is determined by niche difference or competitive ability difference. Our results suggest that the hierarchical approaches can serve as a useful alternative to species-by-species approach for estimating competition coefficients in tree communities.

**Key words:** community modeling; competitive ability; competitive hierarchy; hierarchical Bayes; interspecific interactions; limiting similarity; neighborhood competition; tree demography.

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† **E-mail:** jeyms23@gmail.com

## INTRODUCTION

Quantifying the strength of competition and understanding how it translates into consequences at the community level are among the central challenges in plant ecology (Freckleton et al. 2009). In tree communities, competition strength has often been quantified by means of neighborhood analysis based on the neighborhood competition index (NCI) (Canham et al. 2004, Uriarte et al. 2004a, b). Neighborhood analysis is built upon a statistical model in which the strength of tree competition is expressed as a function of species identity, stem size, and spatial configura-

tion of individuals. The distinct feature of NCI is that it incorporates a species-specific competition coefficient  $\lambda_{xy}$  that multiplies the per-capita influence of a neighboring tree on a target tree (Canham et al. 2006). This feature allows empirical estimation of competition strength between the target tree of species  $x$  and the neighboring tree of species  $y$ . Estimation of  $\lambda_{xy}$  provides a basis to understand the role of tree competition in some of the important ecological issues, including the processes driving functional and phylogenetic diversity (Uriarte et al. 2010, Kunstler et al. 2012, Lasky et al. 2014) and forest dynamics under climate change (Gómez-Aparicio et al. 2011).

In previous neighborhood analyses, the competition coefficients  $\lambda_{xy}$  of each combination of species ( $[x, y] = [1, 1], [1, 2], \dots, [n, n]$ ) have been estimated separately using each pairwise interaction found in a data set (e.g., Canham et al. 2004, 2006, Uriarte et al. 2004a, b, 2010, Coates et al. 2009, 2013, Baribault and Kobe 2012, Das 2012). Under this species-by-species approach, however, target species have often been restricted to major species with sufficiently large sample sizes. That is, rare species with sample sizes less than a prospectively defined threshold have been discarded from analyses (e.g., Gómez-Aparicio et al. 2011, Das 2012) or pooled into groups (e.g., Uriarte et al. 2004b, Coates et al. 2013). Estimation of  $\lambda_{xy}$  in species-rich communities has been especially difficult, because the number of possible pairwise combinations increases in proportion to the square of the number of component species, making the collection of adequate sample sizes for all the combinations intractable.

In this study, we use a hierarchical Bayesian approach to deal with this issue. A hierarchical approach enables independent estimation of the species-specific parameters, while taking into account the mean and variance of a common distribution that is shared across the entire community (Royle and Dorazio 2008). This advantage leads to a more efficient modeling framework that does not require a priori pooling of species and allows for the inclusion of rare species in the analysis while properly accounting for their differences in sample size (Zipkin et al. 2009, Comita et al. 2010, Yamaura et al. 2011). The hierarchical approach is by no means a way to derive more “precise” estimations of  $\lambda_{xy}$  compared to the species-by-species approach, but may contribute to effectively draw out information from a given data set by imposing appropriate constraints to the model.

Here, we develop a hierarchical modeling framework for neighborhood analysis to estimate competition coefficients  $\lambda_{xy}$ . We build multiple models in each of which the competitive strength is determined by niche overlap between species (i.e., competition driven by limiting similarity; MacArthur and Levins 1967), competitive ability difference among species (i.e., competitive hierarchy; Goldberg and Landa 1991), or is independent of species identity (i.e., neutral; Goldberg and Werner 1983). Our specific objectives were to first examine whether the competitive strength of all combina-

tions of species can be estimated by adopting a hierarchical structure for the competition coefficient  $\lambda_{xy}$ . We then compare the hierarchical community models with the conventional species-by-species models based on model selection.

## METHODS

We first describe the model structure and subsequently apply it to an actual field data set. We examine seven candidate models defined by the combinations of the types of competition (neutral, limiting similarity, and competitive hierarchy) and parameter structures (species-by-species and hierarchical community). We build these models by modifying our previous neighborhood model (Tatsumi et al. 2013) in which we focused only on competitive hierarchy and examined competitive effect but not competitive response (see below for the definitions of competitive effect and response). Our models require the use of tree census data in which the diameters at breast height (DBH) of mapped trees within a research plot(s) are measured repeatedly.

### Statistical models

To estimate the species-specific competition coefficients, we developed neighborhood models in which the relative DBH growth rate is expressed as a function of the target tree’s DBH and competition from neighbors. We used DBH growth rate as the response variable because the majority of previous NCI analyses have used this demographic parameter as a measure of competitive outcome (e.g., Baribault and Kobe 2012, Das 2012, Coates et al. 2013). DBH growth rate was defined as the difference in DBH between consecutive measurements. Based on the frequency distribution of DBH growth rate (Appendix S1), we assumed that the natural logarithm of DBH growth rate of target tree  $i$  of species  $s$  in plot  $p$  ( $G_{isp}$ , cm) would follow a normal distribution:

$$\ln(G_{isp}) \sim \mathcal{N} \left[ \ln(\bar{G}_{isp}), \sigma_1 \right] \quad (1)$$

where  $\bar{G}_{isp}$  is the expected DBH growth rate (cm) of target tree  $i$  of species  $s$  in plot  $p$  and  $\sigma_1$  is the variance.

We used the Gompertz growth function (Gompertz 1825, Zeide 1993) to express the effects of the target tree's DBH and competition from neighbors on the relative DBH growth rate:

$$\ln\left(\frac{\bar{G}_{isp}}{D_{isp}^{[t]}T_{isp}}\right) = \alpha_s^{[0]} + \alpha_s^{[1]}D_{isp}^{[t]} - \text{NCI}_{isp} + \psi_p \quad (2)$$

where  $D_{isp}^{[t]}$  is the DBH (cm) of target tree  $i$  of species  $s$  in plot  $p$  (the superscript  $[t]$  stands for *target*),  $T_{isp}$  is the number of years between consecutive measurements,  $\text{NCI}_{isp}$  is the neighborhood competition index for target tree  $i$  of species  $s$  in plot  $p$  (described in detail below),  $\alpha_s^{[0]}$  and  $\alpha_s^{[1]}$  are parameters for species  $s$ , and  $\psi_p$  is a random parameter for plot  $p$ . The random parameter  $\psi_p$  can be excluded when the data were collected in a single plot. The parameters  $\alpha_s^{[0]}$  and  $\alpha_s^{[1]}$  were estimated using either a species-by-species approach or a hierarchical community approach. For the former approach, the parameters were expressed as follows:

$$\alpha_x^{[0]} \sim \mathcal{N}(0, 10000), \alpha_x^{[1]} \sim \mathcal{N}(0, 10000) \quad (3)$$

where  $x = 1, 2, \dots, n$ . Here, the parameters  $\alpha_x^{[0]}$  and  $\alpha_x^{[1]}$  were estimated individually for  $n$  studied species on the assumption that species-specific responses of growth rate to DBH are independent of one another. For the hierarchical community approach, the parameters were expressed as follows:

$$\begin{aligned} \alpha_x^{[0]} &\sim \mathcal{N}(\bar{\alpha}_0, \sigma_2), \bar{\alpha}_0 \sim \mathcal{N}(0, 10000) \\ \alpha_x^{[1]} &\sim \mathcal{N}(\bar{\alpha}_1, \sigma_3), \bar{\alpha}_1 \sim \mathcal{N}(0, 10000) \end{aligned} \quad (4)$$

where  $x = 1, 2, \dots, n$ ; and  $\sigma_2$  and  $\sigma_3$  are variances for the parameters  $\alpha_s^{[0]}$  and  $\alpha_s^{[1]}$ , respectively. Here, the parameters  $\alpha_s^{[0]}$  and  $\alpha_s^{[1]}$  were estimated individually for each species but drawn from common distributions with hyperparameters  $\bar{\alpha}_0$  and  $\bar{\alpha}_1$ , respectively.

By modifying the functional form of NCI step by step, we tested different hypotheses concerning the competition coefficient  $\lambda_{xy}$ . We used an index developed by Canham et al. (2004) and Uriarte et al. (2004a, b) as a basis for all NCI equa-

tions. This index expresses the total competitive effects on a target tree as a summation of the effects of individual neighboring trees. Neighboring trees were defined as those individuals located within 10 m of a target tree based on previous findings that the competitive effect of neighbors beyond this distance is negligible (e.g., Thorpe et al. 2010, Tatsumi and Owari 2013) (this assumption was also confirmed by our analyses; see *Results*). Trees within 10 m of the plot boundary were defined to act as neighbors but not as target trees to avoid edge effects.

The simplest hypothesis we tested assumed that the competition strength between a target tree and a neighbor is independent of their species identities (i.e., neutral; Goldberg and Werner 1983) and determined by their DBH and the distance between them:

$$\text{NCI}_{isp} = \lambda \exp(\beta_1 D_{isp}^{[t]}) \sum_j \exp[\beta_2 \log(D_j^{[n]}) + \beta_3 M_j] \quad (5)$$

where  $D_{isp}^{[t]}$  is the DBH (cm) of target tree  $i$  of species  $s$  in plot  $p$ ;  $D_j^{[n]}$  is the DBH (cm) of neighboring tree  $j$  (the superscript  $[n]$  stands for *neighbor*);  $M_j$  is the distance (m) between the target tree and neighboring tree  $j$ ; and  $\lambda$ ,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$  are parameters. The prior distribution of the logarithm of parameter  $\lambda$  was defined as a noninformative normal distribution:  $\ln(\lambda) \sim \mathcal{N}(0, 10000)$ . We refer to Eq. 5 as the "neutral NCI."

Next, we tested whether the competition strength between a target tree and a neighbor would vary by the pairwise combination of their species identities. The rationale for this hypothesis is that the strength of competition between two species is potentially determined by their niche similarity (MacArthur and Levins 1967, Kunstler et al. 2012). We tested this hypothesis by incorporating a parameter  $\lambda_{s,S_j}^{[l]}$  (the superscript  $[l]$  stands for *limiting similarity*) into the model:

$$\text{NCI}'_{isp} = \exp(\beta_1 D_{isp}^{[t]}) \sum_j \lambda_{s,S_j}^{[l]} \exp[\beta_2 \log(D_j^{[n]}) + \beta_3 M_j] \quad (6)$$

where,  $S_j$  is the identification code for the species identity of neighboring tree  $j$  ( $S_j = [1, 2, \dots, n]$ ). Here, the per-capita effect of neighboring tree  $j$  of species  $S_j$  on target tree  $i$  of species  $s$  is multiplied by the competition coefficient  $\lambda_{s,S_j}^{[l]}$ . The

magnitude of  $\lambda_{s,S_j}^{[l]}$  represents the competition strength between species  $s$  and  $S_j$ . The coefficient was defined to take an equal value under the same combination of subscripts (e.g.,  $\lambda_{1,2}^{[l]} = \lambda_{2,1}^{[l]}$ ). This definition reflects the assumption that the competition strength is driven by the niche similarity of a given pair of species, irrespective of which individual is the target tree or the neighbor. We refer to Eq. 6 as the “limiting similarity NCI.” The competition coefficients  $\lambda_{s,S_j}^{[l]}$  were estimated using either a species-by-species approach or a hierarchical community approach. For the former approach, the coefficients were expressed as follows:

$$\ln(\lambda_{x,y}^{[l]}) \sim \mathcal{N}(0, 10000) \quad (7)$$

where  $[x, y] = [1, 1], [1, 2], \dots, [n, n]$ . For the hierarchical community approach, the coefficients were expressed as follows:

$$\ln(\lambda_{x,y}^{[l]}) \sim \mathcal{N}[\ln(\bar{\lambda}_l), \sigma_4], \ln(\bar{\lambda}_l) \sim \mathcal{N}(0, 10000) \quad (8)$$

where  $[x, y] = [1, 1], [1, 2], \dots, [n, n]$ ;  $\bar{\lambda}_l$  is a hyperparameter (the subscript  $l$  stands for *limiting similarity*); and  $\sigma_4$  is the variance for the coefficient  $\lambda_{x,y}^{[l]}$ .

Finally, we tested whether the competition strength is determined by the positions of species on a hierarchy of competitive ability (Goldberg and Landa 1991, Kunstler et al. 2012). Competitive ability can be divided into competitive effect and response, where the competitive effect is the ability to suppress other individuals and the competitive response is the ability to avoid being suppressed (sensu Goldberg and Landa 1991). We tested this hypothesis by incorporating parameters  $\lambda_{S_j}^{[e]}$  (the superscript  $[e]$  stands for *effect*) and  $\lambda_s^{[r]}$  (the superscript  $[r]$  stands for *response*) into the model:

$$\text{NCI}_{isp}'' = \lambda_s^{[r]} \exp(\beta_1 D_{isp}^{[l]}) \sum_j \lambda_{S_j}^{[e]} \exp[\beta_2 \log(D_j^{[m]}) + \beta_3 M_j] \quad (9)$$

Here, the competition coefficients,  $\lambda_{S_j}^{[e]}$  and  $\lambda_s^{[r]}$ , determine the interspecific difference in the com-

petitive effect and response, respectively. The magnitude of  $\lambda_{S_j}^{[e]}$  represents the strength of the competitive effect of neighboring tree  $j$  of species  $S_j$ . Larger  $\lambda_{S_j}^{[e]}$  indicates stronger competitive effect. The magnitude of  $\lambda_s^{[r]}$  represents the susceptibility of target tree  $i$  of species  $s$  to competition. Larger  $\lambda_s^{[r]}$  indicates higher susceptibility to competition. We refer to Eq. 9 as the “competitive hierarchy NCI.” The competition coefficients,  $\lambda_{S_j}^{[e]}$  and  $\lambda_s^{[r]}$ , were estimated using either a species-by-species approach or a hierarchical community approach. For the former approach, the coefficients were expressed as follows:

$$\lambda_1^{[e]} = \lambda_1^{[r]}, \ln(\lambda_1^{[e]}) \sim \mathcal{N}(0, 10000) \quad (10)$$

$$\ln(\lambda_y^{[e]}) \sim \mathcal{N}(0, 10000), \ln(\lambda_x^{[r]}) \sim \mathcal{N}(0, 10000)$$

where  $x = 2, 3, \dots, n$ ;  $y = 2, 3, \dots, n$ . Here, parameters  $\lambda_1^{[e]}$  and  $\lambda_1^{[r]}$  (i.e., competitive effect and response of ‘species 1’) were defined to take the same value so that parameters  $\lambda_{S_j}^{[e]}$  and  $\lambda_s^{[r]}$  could be distinguished in the parameter estimation process. This definition does not impose any constraint to the model but was required because the both parameters  $\lambda_{S_j}^{[e]}$  and  $\lambda_s^{[r]}$  in Eq. 9 are multiplication coefficients. For example, when  $\lambda_1^{[e]} \times \lambda_1^{[r]} = 100$ , they can be estimated  $\lambda_1^{[e]} = \lambda_1^{[r]} = 10$  given the above definition. Without it, they can take any combination of values (e.g.,  $\lambda_1^{[e]} = 1$  and  $\lambda_1^{[r]} = 100$ ;  $\lambda_1^{[e]} = 20$  and  $\lambda_1^{[r]} = 5$ ). Parameters  $\lambda_x^{[e]}$  and  $\lambda_y^{[r]}$  for the rest of the species ( $x, y \geq 2$ ) are determined as values relative to  $\lambda_1^{[e]}$  and  $\lambda_1^{[r]}$ . Note that parameters  $\lambda_x^{[e]}$  and  $\lambda_y^{[r]}$  for the rest of the species does not have to take a same value (e.g.,  $\lambda_2^{[e]}$  and  $\lambda_2^{[r]}$  does not have to be equal).

For the hierarchical community approach, the coefficients were expressed as follows:

$$\ln(\lambda_x^{[e]}) \sim \mathcal{N}(\bar{\lambda}_h, \sigma_5), \ln(\lambda_y^{[r]}) \sim \mathcal{N}(\bar{\lambda}_h, \sigma_6) \quad (11)$$

$$\ln(\bar{\lambda}_h) \sim \mathcal{N}(0, 10000)$$

where,  $x = 1, 2, \dots, n$ ;  $y = 1, 2, \dots, n$ ;  $\bar{\lambda}_h$  is a hyperparameter (the subscript  $h$  stands for *hierarchical competition*); and  $\sigma_5$  and  $\sigma_6$  are the variances for the coefficients  $\lambda_x^{[e]}$  and  $\lambda_y^{[r]}$ , respectively. Here,  $\lambda_x^{[e]}$  and  $\lambda_y^{[r]}$  were defined to take the identical mean value  $\bar{\lambda}_h$  so that they could be distinguished in the parameter estimation process. See Appendix

S2 for the prior distributions of the parameters  $\beta_1$ – $\beta_3$ ,  $\sigma_1$ – $\sigma_6$ , and  $\psi_p$ .

#### Parameter estimation and model selection

We fitted seven candidate models (Table 1) defined by the combinations of NCI types (“without NCI,” “neutral NCI,” “limiting similarity NCI,” and “competitive hierarchy NCI”) and parameter structures (“species-by-species” and “hierarchical community”) to the data. Here, models 1 and 2 (models without NCI) are models in which NCI of Eq. 2 were set to zero. The posterior distributions of the parameters were estimated using the Markov chain Monte Carlo (MCMC) method implemented by the OpenBUGS 3.2.2 (Lunn et al. 2009) via the ‘R2OpenBUGS’ package (Sturtz et al. 2005) in R 3.1.0 (R Core Team, 2014). For each model, we obtained posterior samples using three independent MCMC samplings, in each of which 400 values were sampled at a 200-step interval after a burn-in period of 2000 MCMC steps. We judged that the MCMC calculation had converged when the  $\hat{R}$  values for all parameters within a model were  $<1.1$  (Gelman et al. 2013). In our preliminary analyses of model 4, parameter  $\lambda_{x,y}^{[l]}$  did not converge ( $\hat{R} \geq 1.1$ ) for some of the species-pairs. Therefore, for model 4, we gradually grouped these species-pairs into *other species-pairs* in order of increasing sample size until parameters  $\lambda_{x,y}^{[l]}$  converged for all species-pairs. We used the deviance information criterion (DIC; Spiegelhalter et al. 2002) for model selection. The model with lower DIC was considered better in pairwise comparisons.

#### Model application

We applied the models to tree census data collected in 17 permanent plots (0.22–0.53 ha) located in a cool-temperate forest of northern Japan. The forest mainly consists of mixed conifer–broadleaf stands with evergreen conifer and deciduous broadleaved species. We used DBH data ( $\geq 5.0$  cm DBH) collected in the period 1998–2012 at 4- or 5-yr intervals. The plots contained 38 tree species in total. The observed ranges of DBH, tree density, and stand basal area (BA) were 5.0–95.8 cm, 553.8–2129.1 trees/ha, and 29.9–55.5 m<sup>2</sup>/ha, respectively. See Appendix S3 for details of the study site and data.

## RESULTS

The MCMC calculation converged sufficiently ( $\hat{R} < 1.1$ ) for models 1–3 and 5–7. In model 3, which used the neutral NCI, the estimated value of  $\lambda$  ranged from 0.005 to 0.015, with a mean of 0.009 (Fig. 1a). For model 4, which used limiting similarity NCI and the species-by-species approach, the calculation converged when all data other than the species-pair with the largest sample size were pooled into *other species-pairs*. That is, only two values of  $\lambda_{x,y}^{[l]}$  could be estimated in model 4 (Fig. 1b). On the other hand, model 5, which used the hierarchical community approach, allowed us to estimate  $\lambda_{x,y}^{[l]}$  for all combination of species-pairs found in the data set (535 species-pairs; note that the maximum possible number of pairs was 741 [ $38 + {}_{38}C_2$ ] but the sample sizes for 206 pairs were zero). Among these 535 species-pairs, 10 had 95% credible intervals (CI) that did not overlap the mean value of the community-level hyperparameter  $\tilde{\lambda}_l$  (Fig. 1c).

A large difference in parameter estimates was observed between the two models that used the competitive hierarchy NCI (models 6 and 7). The estimates of  $\lambda_x^{[e]}$  and  $\lambda_x^{[r]}$  approached zero for model 6, which used the species-by-species approach (Fig. 1d, e), whereas those for model 7, which used the hierarchical community approach, did not (Fig. 1f, g). Among the 38 species studied, the 95% CI of  $\lambda_x^{[e]}$  for four species (Fig. 1f) and that of  $\lambda_y^{[r]}$  for three species (Fig. 1g) did not overlap the mean value of the hyperparameter  $\tilde{\lambda}_l$ . Under the hierarchical community approach, the estimates of rare species and rare species-pairs remained in the vicinity of group averages (Fig. 1c, f, g), reflecting their small sample sizes.

Models 5 and 7, which used the hierarchical community approach to estimate the competition coefficients, had the two smallest DIC values. This was followed in rank order by model 3, which assumed no interspecific differences, and models 4 and 6, which used the species-by-species approach (Table 1). The result that the limiting similarity model (model 5) and the competitive hierarchy model (model 7) were selected over the neutral model (model 3) indicates that the species identities of individuals affect the outcome of competition in our study site.

Table 1. Definitions, descriptions, and the deviance information criteria (DIC) of candidate models.

Model number	Equation numbers	Definitions			Model description	DIC†
		Method used to estimate parameters $\alpha^{[0]}$ and $\alpha^{[1]}$	Type of neighborhood competition index (NCI)	Method used to estimate competition coefficient $\lambda$		
1	2 and 3	Species-by-species	Without NCI	n.a.	Intercept $\alpha^{[0]}$ and slope parameter $\alpha^{[1]}$ are estimated using the species-by-species approach.	9177
2	2 and 4	Hierarchical community	Without NCI	n.a.	Same with model 1 except that the parameters are estimated using the hierarchical community approach.	9164
3	2, 4, and 5	Hierarchical community	Neutral	No interspecific difference	Competition strength between target trees and neighbors is independent of their species identities. The strength of competition is determined by competition coefficient $\lambda$ .	8999
4	2, 4, 6, and 7	Hierarchical community	Limiting similarity	Species-by-species	Competition strength is driven by the extent of niche overlap between two species. Coefficient $\lambda_{x,y}^{[1]}$ determines the strength of competition between species $x$ and $y$ , and is estimated for each species-pair ( $[x, y] = [1, 1], [1, 2], \dots, [n, n]$ ). The species-by-species approach is used for estimating $\lambda_{x,y}^{[1]}$ .	9015
5	2, 4, 6, and 8	Hierarchical community	Limiting similarity	Hierarchical community	Same with model 4 except that $\lambda_{x,y}^{[1]}$ is estimated using the hierarchical community approach.	<b>8757</b>
6	2, 4, 9, and 10	Hierarchical community	Competitive hierarchy	Species-by-species	Competition strength is driven by the difference in competitive ability among species. Coefficients $\lambda_x^{[e]}$ and $\lambda_y^{[r]}$ determine the magnitude of competitive effect and response, respectively. Coefficient $\lambda_x^{[e]}$ represents the strength of the competitive effect of neighboring trees of species $x$ . Coefficient $\lambda_y^{[r]}$ represents the response of target trees of species $y$ to competition. The two coefficients are estimated for each species ( $x = 1, 2, \dots, n; y = 1, 2, \dots, n$ ). The species-by-species approach is used for estimating $\lambda_x^{[e]}$ and $\lambda_y^{[r]}$ .	9164
7	2, 4, 9, and 11	Hierarchical community	Competitive hierarchy	Hierarchical community	Same with model 4 except that $\lambda^{[e]}$ and $\lambda^{[r]}$ are estimated using the hierarchical community approach.	8921

† The models with smallest and second smallest DIC values are indicated in bold and italic, respectively.

The magnitude of NCI was significantly affected by target and neighbor DBH values and by the distances between targets and neighbors (Fig. 2). For example, parameter estimates of the best model (model 5) (Appendix S4) showed that the per-capita competition strength a tree with a 5.0-cm DBH receives was 20.6-fold greater than that of a tree with a 95-cm DBH receives (Fig. 2a). The competitive effect of a neighbor with a 95-cm DBH was 48.0-fold greater than

that of a neighbor with a 5-cm DBH (Fig. 2b). A neighbor located 0.1 m from a target tree had 21.9-fold greater effect than a neighbor located 10 m away (Fig. 2c). Neighbors within a 10-m radius exerted the great majority of competitive effect, providing support for our use of this radius size in the analyses.

The BUGS codes for models with the two smallest DIC values (models 5 and 7) are provided as Supplement S1.

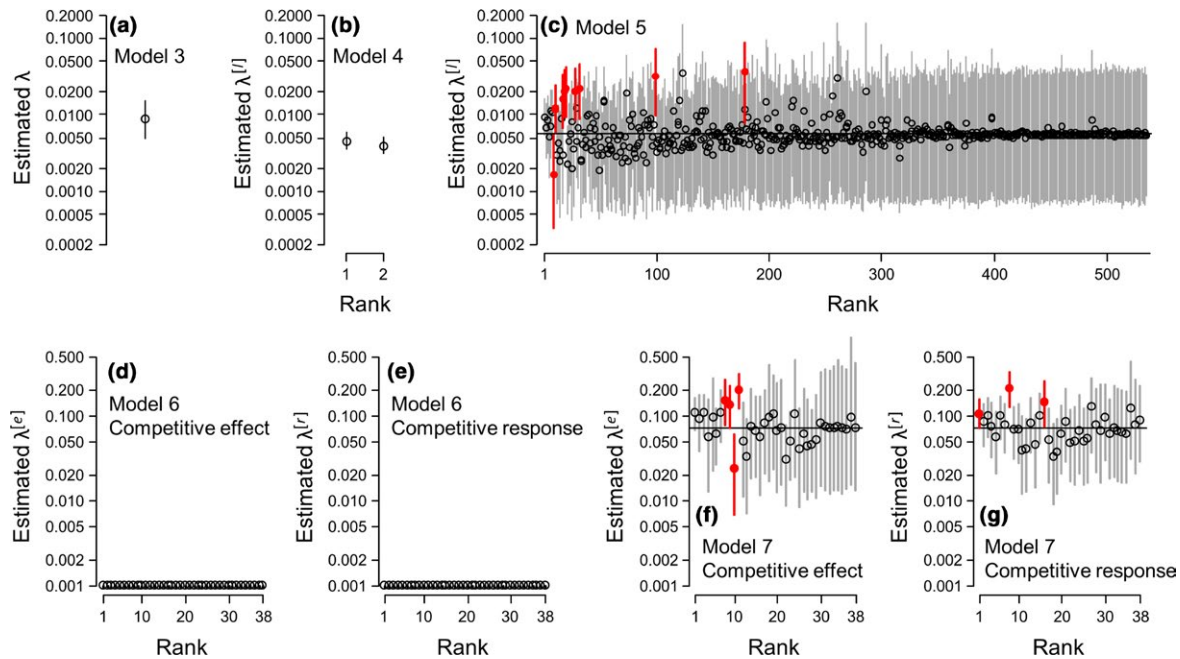


Fig. 1. Estimates of competition coefficients for models 3–7. See Table 1 for definitions of the models. The horizontal axes show the rank order of species or species-pairs based on sample sizes. Horizontal bars in panels c, f, and g indicate mean values of the community-level hyperparameters. Circles and vertical bars are mean values and 95% credible intervals (CI) of the posterior distributions, respectively. The red filled circles and red vertical bars in panels c, f, and g show that the 95% CI of the posterior distributions do not overlap the mean value of the hyperparameter. (a) Estimate of competition coefficient  $\lambda$  for the neutral NCI model; there is only one value because the coefficient  $\lambda$  was defined to be equal among tree species. (b) Estimates of  $\lambda^{[l]}$  for the limiting similarity NCI model using species-by-species approach; only two values are provided because the calculation converged when all data other than the species-pair with the largest sample size were pooled into *other species-pairs*. (c) Estimates of  $\lambda^{[l]}$  (535 species-pairs) for the limiting similarity NCI model using hierarchical community approach. (d and e) Estimates of  $\lambda^{[e]}$  and  $\lambda^{[r]}$  (38 species), respectively, for the competitive hierarchy NCI model using species-by-species approach. (f and g) Estimates of  $\lambda^{[e]}$  and  $\lambda^{[r]}$  (38 species), respectively, for the competitive hierarchy NCI model using hierarchical community approach.

## DISCUSSION

Our method offers a new framework for efficiently estimating the strengths of competitive interactions in tree communities. Previous neighborhood analyses based on conventional species-by-species approach had limited ability in estimating competition coefficients of rare species with small sample sizes (e.g., Uriarte et al. 2004b, Gómez-Aparicio et al. 2011, Das 2012, Coates et al. 2013). Such limitation was also observed in our analyses based on the species-by-species approach; coefficients of only two of the 535 species-pairs were estimated successfully under the limiting similarity NCI

(model 4; Fig. 1b). In contrast, the hierarchical community approach allowed us to estimate competition coefficients for all species-pairs including rare ones (model 5; Fig. 1c). For the competitive hierarchy NCI, the species-by-species approach failed to detect competitive interactions (model 6; Fig. 1d, e), whereas the hierarchical community approach detected considerable interactions (model 7; Fig. 1f, g). Moreover, the hierarchical community models were selected over the species-by-species models as a result of model selection, in either cases of limiting similarity NCI and competitive hierarchy NCI (Table 1). The hierarchical community approach simultaneously estimates

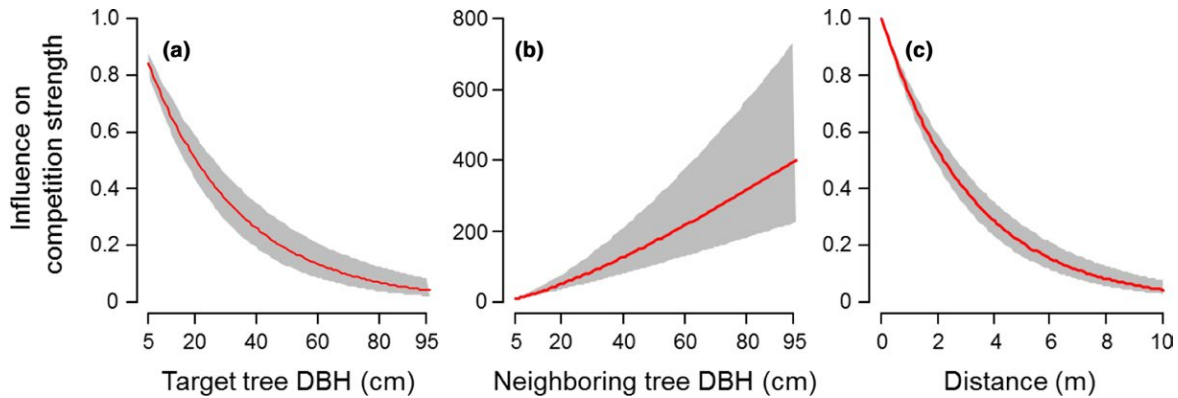


Fig. 2. The effects of (a) target tree DBH, (b) neighboring tree DBH, and (c) the distance between the target tree and the neighboring tree on competition strength. Each panel shows how the relative strength of competition changes in response to the value of the variable on the  $x$ -axis when the values of the other two variables were held constant. The three panels correspond to the three terms in Eq. 6: (a)  $\exp(\beta_1 D^{[l]})$ , (b)  $(D^{[n]})^{\beta_2}$ , and (c)  $\exp(\beta_3 M)$ . The model with the smallest deviance information criterion value (model 5, see Table 1) and its parameter estimates (Appendix S4) were used for predictions. Red lines and shaded areas represent the mean values and 95% credible intervals, respectively.

species-specific parameters and the hyperparameter that constrains their variance (Royle and Dorazio 2008). The present analyses successfully demonstrate an example that imposing such constraints can allow us to estimate the competition coefficients for all species and species-pairs and may contribute to the overall model. This result, however, does not necessarily indicate that the hierarchical approach yields more “precise” estimates than the species-by-species approach, as is clear from the estimates of rare species and species-pairs being drawn toward the mean value of the hyperparameter (Fig. 1c, f, g). Large sample size and models with minimum constraints are always preferable. Nevertheless, our results suggest that, at least in some cases, the hierarchical approach can serve as a useful alternative to species-by-species approach for estimating competition coefficients under a given data.

Our modeling framework also has a potential as a tool for testing different hypotheses about competition and its consequence in species coexistence. In this study, we developed multiple models that each assumes different competition mechanisms: neutral (Goldberg and Werner 1983), limiting similarity (MacArthur and Levins 1967), and competitive hierarchy (Goldberg and Landa 1991). As a result of model selection, the

limiting similarity model and the competitive hierarchy model using the hierarchical community approach (models 5 and 7) were selected over the neutral model (model 3) (Table 1). This indicates that not only the stem size and spatial configuration of trees (Fig. 2) but also their species identity affects the outcome of individual-level competition in our study site. Moreover, in the coexistence theory proposed by Chesson (2000), competition driven by limiting similarity fosters diversity by making species to have higher population growth rates when rare than common, whereas competitive hierarchy among species causes competitive exclusion of inferior species and limits coexistence (Adler et al. 2007, Hille RisLambers et al. 2012). Our result that the limiting similarity model (model 5) was selected as the best model (Table 1) thus indicates that competition plays an important role in promoting coexistence in our study site, and this may partly explain the relatively high species richness.

The findings from this study, however, should be generalized carefully. In our analyses, the species-by-species approach could only estimate competition coefficients for 2 of 535 species-pairs under the limiting similarity NCI (Fig. 1b) and could not detect competitive interactions under the competitive hierarchy NCI (Fig. 1d, e). However, previous neighborhood analyses that used



the same approach, but mostly larger data set than ours, were able to quantify several tens of pairwise interactions which significantly differed from zero (e.g., Uriarte et al. 2004a, Canham et al. 2006, Coates et al. 2009, 2013). This indicates that whether it is more appropriate to adopt the hierarchical community approach or the less constrained, species-by-species approach depends on the quantity and quality of a given data. Therefore, the extent to which the sample size as well as forest attributes (e.g., species richness, spatial distribution of individuals) affect the outcome the two approaches needs to be examined in future studies. Moreover, further researches using multiple measures of model selection are required, given the potential instabilities in DIC (Gelman and Hill 2006) which was used in this study. Finally, while the present study tested the three competition mechanisms (i.e., neutral, limiting similarity, and competitive hierarchy) separately given the computational simplicity, these mechanisms are known to act simultaneously in regulating community dynamics (Lasky et al. 2014). Quantifying their relative importance through modifications of the current model could further improve our understanding of tree competition and its consequences in community dynamics.

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